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THE ORIGIN OF CERATOPSIAN HORN-CORES

BY BARNUM BROWN AND ERICH M. SCHLAIKJER[1]

INTRODUCTION

Two monographs and a large number of shorter papers represent the many valuable contributions to the study of the ceratopsian dinosaurs. There are, however, still several important problems that remain unsolved. One of these, about which there is considerable disagreement, is the problem of the origin of the nasal and brow horn-cores.

It is quite clear that in some genera the nasal horn-core is formed by the upgrowth of the nasal bones, and the question is, whether an archaic member such as *Brachyceratops* with a nasal horn-core so formed could be the progenitor of the more progressive types in which the nasal horn-core is suturally distinct from the nasal bones. Also, is the distinct nasal horn-core, such as that of *Triceratops*, composed of a single element or of a pair of fused elements? The question of the origin of the brow horn-cores is whether they develop as distinct elements homologous with the epijugals, epoccipitals, and the distinct nasal horn-core, or are outgrowths of the postorbital (postfrontal) bones.

In connection with our intensive study of *Protoceratops*, the results of which are soon to be published, we have had occasion to restudy much of the previously described ceratopsian material. From this study we have obtained results, presented herewith, that have considerable bearing on the problem of the origin of the nasal and brow horn-cores.

The drawings in this paper were made by Mr. Alastair Brown of the Museum's staff of artists.

THE NASAL HORN-CORES

The changes that take place in the nasal bones in *Protoceratops* from the very immature to the fully adult skull throw much light on the problem of the origin of the ceratopsian nasal horn-core. The nasals of the very young individual are quite short, fairly deep, and are rather flat on the dorsal surface. In the older skulls, however, they become proportionately elongated, assume deeper proportions, and begin to arch upward about midway back so that in the fully adult male skull the nasals form a pronounced horn-like structure with the grain of the bone tending toward the apex.

On the dorsal surface of the nasals, there is a longitudinal median groove that extends throughout their sutural length. In the young and early adult skulls this groove continues back onto the anterior projection of the frontals, but in the older individuals it is confined to the nasal bones. In the smallest skulls, this groove is broad and very shallow. With age, it becomes deeper and narrower, although there is some variability in deepness and narrowness in both what we consider as male and female skulls. In skulls of the same size, however, it does seem to be deeper and narrower in the male. The development of this groove, together with the proportionate deepening and narrowing of the nasals and the marked upward arching of them into an incipient horn-core is of considerable morphological significance. As the nasal bones arch upward, the median groove becomes very constricted between the apices of the convexities. This

[1] Assistant Professor of Geology and Paleontology, Brooklyn College, New York City.

arching of the nasals, and the fact that the grain of the bones tends toward the apices, suggests that the nasals probably bore one, or possibly two horn-like epidermal protuberances, although there is no direct evidence that ossicles were present.

In the light of this evidence, it seems reasonable to conclude, therefore, that the arching of the nasals in *Protoceratops* represents the beginning of a nasal horn-core in the ceratopsians. The only change necessary for giving rise to the next advanced stage, as seen in *Brachyceratops*, would be for the nasals to continue to grow upward into a pronounced laterally flattened nasal horn-core.

Gilmore (1917, pp. 37–38) regards such a nasal horn-core, composed of the nasal bones, and not of a distinct element, as of considerable taxonomic importance. In discussing the relationship of *Brachyceratops* he says, "That the genus *Brachyceratops* represents one of the more generalized forms of the Ceratopsidae is apparent; that it cannot be included in either the *Ceratops–Torosaurus* or the *Eoceratops–Triceratops* phylum is also evident, for it is hardly conceivable that an animal like *Brachyceratops*, having a nasal horn split longitudinally by suture and an outgrowth from the nasal bones, could be the progenitor of later ceratopsians having this horn developed from a center of ossification distinct from the nasal bones." This reasoning now seems inadequate for eliminating *Brachyceratops* as the structural progenitor of the later ceratopsians. In the first place, aside from an evaluation of the nasal horn-core, this genus seems to possess no character which would eliminate it from that ancestral position. Secondly, in addition to *Brachyceratops*, a divided nasal horn-core formed entirely or mostly by the nasal bones is known in *Eoceratops*, *Monoclonius* (including *Centrosaurus*), *Anchiceratops*, *Casmosaurus*, and *Arrhinoceratops*. Thirdly, the summit of the left half of the nasal horn-core of *Brachyceratops* bears a small distinct ossicle. Whether or not such an ossicle also was present above the right half of the horn-core cannot be determined since the tip of it is broken away. On the basis of the evidence, however, it would seem logical to conclude that paired ossicles may have been present. This is also suggested by the condition in *Protoceratops*, in which the apices of the nasals are distinct. Even though the apices of the nasal bones in this genus are closely appressed, there is a narrow valley between them and they form two distinct protuberances, which strongly suggests that they each bore a superficial epidermal structure. It seems quite logical to conclude that the ossicle or ossicles (if two were present) above the nasal horn-core of *Brachyceratops* are homologous with the nasal horn-core of a form like *Triceratops* in which it is suturally distinct from the nasal bones.[1] Although whether or not this distinct nasal horn-core of *Triceratops* is made up from two distinct centers of ossification is at present undeterminable, since no known specimen definitely shows a nasal horn-core composed of two elements. Such a conclusion can be based on inference only. *Eoceratops* throws some light on the question. In his description of this genus, Lambe states (1915, p. 6) that on the front of the nasal "facing obliquely outward and forward, there is a shallowly concave sutural surface of concentric outline for the reception of a separate bone which, with its mate and the anterior end of the nasals, formed the nasal horn-core." To these separate ossifications he applied the name "epinasals" and considered their presence as conclusive evidence that the nasal horn-core of *Triceratops* was composed of two elements. On the basis of this meagre evidence such a conclusion seems probable. Nevertheless, that the distinct nasal horn-core may in some forms be composed of one, and in others of two elements, is also a possibility.

A summary of what seems to have been the course of development of the nasal horn-core among the Ceratopsia is as follows:

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[1] That the nasal horn-core in *Triceratops* is a separate element suturally united with the nasals seems unquestionable. Hatcher (1907, p. 33) figures and describes a nasal horn-core, in the University of Chicago collection, which is of a fairly young individual, and in which the basal suture is clearly shown. In the American Museum a large nasal horn-core (No. 5883) of an adult, from the Hell Creek Beds, also shows the basal suture unusually well preserved.

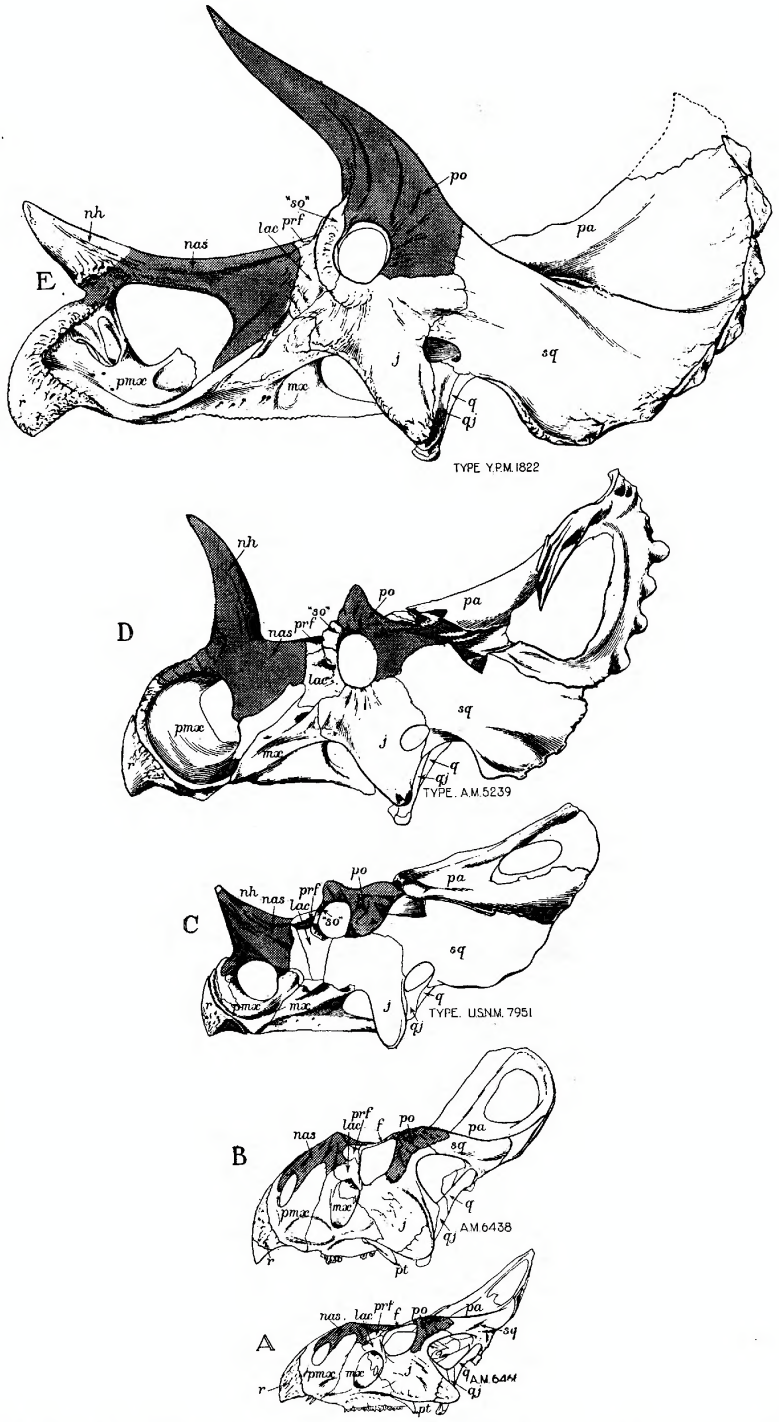

Fig. 1. Structural series of ceratopsian skulls showing the development of horn-cores. A, *Protoceratops andrewsi*. Skull of an adult "male." B, *Protoceratops andrewsi*. Skull of an old "male." C, *Brachyceratops montanensis*. Modified from Gilmore. D, *Monoclonius flexus*. E, *Triceratops prorsus*. Modified from Hatcher, Marsh, and Lull.

1.—A gradual upward arching of the nasals to form, in the adult stage, two well-marked bases for a pair of horn protuberances—the *Protoceratops* stage. This probably was also the condition in *Leptoceratops*, for the only known nasal bones of that genus show a suggestion of the shallow median groove so characteristic in *Protoceratops*.

2.—The further upgrowth of the nasal bones forming a well-developed nasal horn-core, which probably bore a pair of osseous elements. This stage is illustrated by all of the other earlier ceratopsians, although osseous elements (epinasals of Lambe) have been found only in *Brachyceratops* and *Eoceratops*.

3.—A gradual retrogression of the nasal horn-core and an enlargement of the osseous element, or elements, to form a nasal horn-core suturally distinct from the nasal bones as in *Triceratops*. This retrogression of the nasal horn-core, which is composed mainly of the nasal bones, seems definitely associated with the progressive development of the brow horn-cores. Along with these changes, the nasal horn-core assumes a more anterior position on the face. This change of position is the result of differential changes in the individual elements, and alteration of the architecture of the whole face. It seems most closely related to the outgrowth and great enlargement of the brow horn-cores, the downward growth of the postero-lateral wing of the nasal, and a ventral shifting of the anterior ascending part of the premaxillary. This new construction of the face placed the nasal horn in a position so that whatever stresses it may have received were safely transmitted backward and downward around the enlarged narial opening. Moreover, enlargement of the nasal bones at the base of this horn strengthened that area of the nasals which transmitted over the narial opening all of the upward stresses from the beak. (See Fig. 1.)

THE BROW HORN-CORES

The question of whether the brow horn-cores are outgrowths of the postorbitals, or are derived from separate elements homologous with the epoccipitals, epijugals, and the distinct nasal horn-core of *Triceratops*, has received considerable attention.

In discussing the brow horn-cores of *Triceratops*, Hatcher, Marsh, and Lull (1907, p. 32) say, "They rise from the superior and lateral surfaces of the postfrontals [= postorbitals] and may be considered as outgrowths from those bones, the frontals and prefrontals entering but little, if at all, into their composition." Von Huene (1911, p. 156) thinks it probable that they were formed from separate elements, Lambe (1913, p. 113) in his description of the postorbital of *Styracosaurus* says, "Set well back posteriorly on the raised ridge above the eye-opening is a small, shallow, smooth depression, irregularly oval in outline, which indicated the position of an extremely small, or incipient, supraorbital horn-core, which appears to have been present as a separate ossification and to have become detached." Mainly on the basis of these supposed separate elements on the low brow horn-core of *Styracosaurus*, Lambe concluded (1915, p. 22) that, "the supraorbital horn-core is to be regarded, therefore, not as a simple outgrowth from the postfrontal [= postorbital] but as a separate element, in the same category with the epijugal and the epoccipitals and like them to become firmly attached to the underlying element with generally a more or less perfect obliteration of the sutural contact." He goes on to say that, ". . . a more or less distinct basal engirdling groove or constriction is sometimes present as an indication of where coössification has taken place," and that, ". . . foramina or deep pits not infrequently occur at the horn-base and may be regarded as marking the position of a closed suture." On the other hand, Gilmore (1917, p. 11) feels, and quite rightfully it seems, that the low, knob-like brow horn-core of *Brachyceratops* is an outgrowth of the postorbital. The same seems to be true for *Chasmosaurus* as is shown by a splendidly preserved skull (No. 5402) of *C. belli* in the American Museum collections; and by the right postorbital of a young ? *Chasmosaurus* sp. (No. 840), in the collections of the Geological Survey of Canada, which shows the brow horn-core as a low sharply pointed structure that has unquestionably grown out of the postorbital.

In addition to this material, there is in the American Museum an unusually well-preserved postorbital of a very immature specimen of *Triceratops* (No. 5006) collected by the senior writer, from the Hell Creek formation (a Lance equivalent) of Montana in 1906. This rare specimen (Fig. 2) shows conclusively for the first

time that the brow horn-core of *Triceratops* is an outgrowth of the postorbital. Furthermore, it also shows exactly how the upgrowth of the horn-core takes place. Just behind the brow horn-core on the dorsal surface near the posterior margin is a small protuberance which apparently is homologous with the wrinkled surface on the posterior flank of the brow horn-core of a species such as *Triceratops elatus*. The posterior margin of the bone is broken away and thus the transverse cross-section of this incipient horn-like process is revealed. The bone is thickened in this area and a fissure has developed about halfway down in the bone forming a cavity under the process. On the lateral margins of the fissure the normal bone texture is retained. This process originates, therefore, by an upward bulging of the dorsal surface, which leaves a cavity beneath it, that is formed within the bone. The ventral surface is thickened somewhat and forms a floor under the cavity. This process seems to show what was probably the structure of the brow horn-core when it first appeared. From an early beginning such as this, the brow horn-core would continue to develop with the cavity extending up into its base and the floor remaining more or less in the original position. This is exactly what is shown by the brow horn-core itself. The basal portion is hollow yet the floor of the bone is in its original position and forms a rather marked basal plate under the horn-core. As the horn-core increased in size this plate would extend forward and medially to form an important shelf in the skull roof—buried, of course, beneath the brow horn-core and reaching, or nearly so, the median line of the skull. This, apparently, is what von Huene thought was the frontal, which he regarded as buried beneath the roof of the skull.

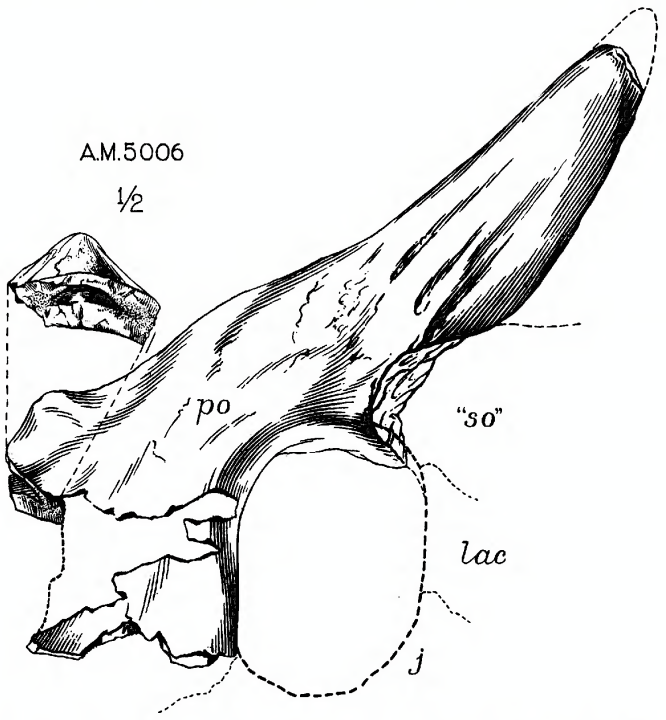

Fig. 2. Postorbital bone of a very young *Triceratops* sp. from the Hell Creek Beds of Montana showing the brow horn-core as an outgrowth of that bone.

On the front and at the base of the horn-core of this Hell Creek specimen there is a

fairly extensive sutural surface for articulation with the "supraorbital." At the infero-internal corner of this suture, there is a smaller sutural surface that faces forward and inward. This is the suture for the prefrontal. As in *Brachyceratops*, therefore, the prefrontal is in contact with the postorbital in *Triceratops*. The frontal suture extends along the inner side of the horn-core base. It is extensive and faces inward. This suture shows that the frontal, at least in the young individual, in *Triceratops* is present in its normal position on the skull surface between the postorbitals. This point will be discussed more fully in a forthcoming paper under the discussion of the frontal.

As summarized in the above discussion, that the brow horn-cores of the ceratopsians are formed by outgrowths of the postorbital bones seems without question. As for the condition seen in *Styracosaurus* in which the horn-like projection of the postorbital shows a "small, shallow, smooth depression, irregularly oval in outline," there are two possible explanations. In the first place, it is possible that this postorbital projection bore a distinct osseous element, as suggested by Lambe, but this by no means proves, or even implies, that this element gave rise to the brow horn-core. Moreover, the evidence shown in *Brachyceratops*, in *Chasmosaurus*, and in the very immature Triceratops postorbital shows convincingly that it did not. In the second place, if the tip of the incipient brow horn-core were broken off or eliminated by decay before petrifaction, such a smooth depression as seen in *Styracosaurus* would probably result. Furthermore, the "basal engirdling groove" and the deep pits at the horn-bose base which Lambe described in *Triceratops* probably are nothing more than demarcations of the zone where the horny sheath of the horn met the skin.

In *Protoceratops*, the postorbital is primitive in position, and in form. Its position is for the most part posterior to the orbit where it forms the front of the narrow and still quite primitive postorbital-squamosal bar. With age, it enlarges, arches quite pronouncedly, and becomes very rugose, thus foreshadowing the change that takes place in the later forms in which brow horn-cores are developed.

This element in *Protoceratops* is of unusual interest, because, in its primitiveness and in the change it undergoes from youth to old age, it shows the first stage of what is perhaps the greatest transformation of any single element in the ceratopsian skull during the evolution of the group. From this primitive stage, the postorbital grows forward, unites with the enlarged palpebral (= "superorbital"), and thus eliminates the frontal and prefrontal from the margin of the orbit. At this stage, as shown by *Brachyceratops*, the dorsal surface protrudes to form an incipient brow horn-core. Apparently the development of the brow horn-core is held in check, at least in the *Monoclonius-Triceratops* line, while the nasal horn-core proceeds to enlarge.—As shown earlier in this paper, this emphasis of the nasal horn development before that of the brow horns is already established in *Protoceratops*.—When a reduction of the nasal horn begins, the brow horns then enlarge and reach their maximum development in *Triceratops* by the close of the Cretaceous (see Fig. 1). In *Triceratops eurycephalus*, the last of the known species (Schlaikjer, 1934), the brow horn-cores have reached extraordinary proportions and the nasal horn-core is reduced to a low base on which rests a small suturally distinct nasal horn.

SUMMARY

1.—In *Protoceratops* the pronounced horn-core-like structure formed by the arching of the nasal bones represents the first stage in the development of the ceratopsian nasal corn-core.

2.—In all of the earlier ceratopsians the nasal horn-core is formed by upgrowth of the nasal bones. This horn-core probably bore a pair of osseous elements, although these elements are known only in two genera.

3. The distinct nasal horn-core suturally united with the nasal bones, as in *Triceratops*, is the homologue of the nasal ossicle or ossicles of the earlier ceratopsians.

4.—The retrogression of the nasal horn with

the enlargement of the osseous element or elements seems definitely associated with the progressive development of the brow horns.

5.—The brow horn-cores are formed by outgrowths of the dorsal portions of the postorbital (postfrontal) bones. Definite evidence of this is shown by the condition in *Brachyceratops*, *Monoclonius*, *Chasmosaurus*, *Styracosaurus*, and the immature *Triceratops*. This development of brow horn-cores is foreshadowed in *Protoceratops*. With age, the postorbitals in this genus become proportionately enlarged, pronouncedly arched, and very rugose.

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